

Sensitivity of native and alien freshwater bivalve species in Europe to climate-related environmental factors

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Abstract. While native freshwater bivalve species are declining, several alien bivalve species have become invasive, thereby impacting ecosystem functioning and services. These biodiversity changes can be attributed to deteriorated water quality, hydro-morphological alterations, and the overarching effect of global change. Therefore, a systematic assessment of the sensitivity of freshwater bivalve species nowadays occurring in European inland waters to environmental factors is urgent. The present study reviewed 493 relevant papers, resulting in 8405 data entries on presence–absence of bivalve species in relation to environmental factors that are affected by global change (i.e., water temperature, water depth, oxygen availability, and flow velocity). From these worldwide field data, minimum and maximum values measured in their habitat and water bodies were selected. In addition, data on laboratory-derived tolerance ranges were collected. Subsequently, novel species sensitivity distributions (SSDs) were derived for each environmental factor using field-based occurrence data and laboratory-derived tolerance ranges, respectively. Species sensitivity distributions for maximum habitat temperature significantly differed between native and alien species. The latter occurred in habitats with higher maximum water temperatures than native species. The increase in water temperatures by global warming will affect a higher percentage of native species than alien species. The ranking of species based on their sensitivity for various environmental factors shows that vulnerable and endangered species have a higher overall sensitivity and are likely to be more affected by climate change. Invasive alien species were found to have a lower overall sensitivity and are thus less affected by climate change further aiding to their invasive nature. The available SSDs allow the ranking of freshwater bivalve species sensitivity to environmental stressors, the prediction of their potential occurrence in freshwater habitats, and the evaluation of management measures to optimize their biodiversity and ecosystem services.

Key words: air exposure; dissolved oxygen; flow velocity; global change; mollusks; species sensitivity distribution (SSD); water depth; water temperature.

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INTRODUCTION

Freshwater bivalve species provide important ecosystem functions and may act as ecosystem engineers (Eriksson et al. 1989, Naimo 1995, Strayer et al. 1999, Vaughn and Hakenkamp 2001, Gutiérrez et al. 2003, Bogan 2008, Sousa et al. 2009, Vaughn 2010, Lopes-Lima et al. 2017). However, freshwater ecosystems are among the most endangered ecosystems in the world (Allan and Flecker 1993, Malmqvist and Rundle 2002, Dudgeon et al. 2006), and therefore, many bivalve species are threatened. This particularly applies for unionid species. Over 200 endemic unionid species are included on the IUCN Red List (Lydeard et al. 2004), on which 37 species have recently become extinct in North America (Bogan 2008) and seven classified as endangered in Europe (Cuttelod et al. 2011).

The decline in native bivalve biodiversity affects ecosystem services, especially when species are lost that fulfill important ecosystem functions which cannot be compensated by invasive alien bivalves (Sousa et al. 2014). Decreasing diversity and density of native freshwater bivalve species has been attributed to overexploitation of water and organisms, water pollution, modification of flow, habitat destruction, introduction of invasive alien species, and the overarching effect of environmental changes caused by climate change (Dudgeon et al. 2006, Vaughn 2010, Lopes-Lima et al. 2014).

Due to climate change and flow modification of rivers and streams, impacts on the physical habitat of bivalve species are expected to increase in the near future. An alteration of the frequency and duration of extremely low and peak discharges and extreme water temperature events in northwestern European rivers are predicted (Van Vliet et al. 2013). These environmental conditions will further affect freshwater bivalve communities (Verbrugge et al. 2012, Collas et al. 2014). Therefore, it is of utmost importance to quantify the effects of climate-related environmental factors on freshwater bivalve species (Santos et al. 2015). Deriving species sensitivity distributions (SSDs) is a common method to quantify the risks of chemical stressors to biodiversity (Del Signore et al. 2016a). These statistical distributions describe variation in species

sensitivity related to a particular environmental factor (Posthuma et al. 2002). Whereas the vast majority of SSD applications are in the field of toxicology, the method also appears to be a promising tool for quantifying the effects of physical parameters (Smit et al. 2008). Species sensitivity distributions have previously been constructed for water temperature and dissolved oxygen for freshwater fish (de Vries et al. 2008, Leuven et al. 2011, Elshout et al. 2013) and for the effects of air exposure due to water-level fluctuation, salinity, and water temperature on freshwater mollusks (Verbrugge et al. 2012, Collas et al. 2014) in order to elucidate climate change-related impacts on the biodiversity of riverine ecosystems.

A comprehensive database concerning the range of occurrence and tolerance of European freshwater bivalve species to environmental factors influenced by climate change, and flow modification was lacking (Lopes-Lima et al. 2017). This data deficiency limits sound biological conservation and reliable impact assessments of climate change for freshwater bivalve species. Therefore, for the first time a systematic data collection and assessment of the range of occurrences and laboratory tolerances of European bivalve species to climate change-related environmental factors are performed, filling current knowledge gaps and data deficiencies. The aim of the present study was to assess ranges of climate-related environmental factors for occurrence of freshwater bivalve species in Europe. The collated species occurrence ranges will be used to answer the following research questions. Do these ranges differ between water body-based and habitat-based environmental factor measurements or between alien and native bivalve species? Which groups of species are most sensitive to climate change impacts?

The scope of the research is limited to environmental factors that may be important for bivalves for functioning and survival and potentially will be influenced by climate change. In this study, “sensitivity” is defined as the species response to a level of a physicochemical property (cf. Knouft and Ficklin 2017). The response can either be occurrence at reported maximum and minimum levels of a physicochemical property in the field or by mortality due to deleterious effects under

laboratory conditions. Exceedance of a sensitivity inevitably results in limitation of the species. Minimum and maximum water temperature of rivers, lakes, and wetlands are expected to increase due to climate change (Quayle et al. 2002, Adrian et al. 2009, Van Vliet et al. 2013). Moreover, increased frequency and duration of extremely low and peak discharges (Lehner and Döll 2001, Van Vliet et al. 2013) require the assessment of species sensitivity to air exposure as a proxy for the risk of desiccation, minimum and maximum flow velocity, and species occurrence in relation to water depth. Additionally, the species sensitivity to oxygen depletion is assessed since oxygen can become a limiting factor at high temperatures during low discharges or in stagnant waters (Baxter 1977, Gagnon et al. 2004).

MATERIALS AND METHODS

Species selection and data collection

A list of 55 native and alien bivalve species occurring in European freshwaters was compiled using several literature sources (Cuttelod et al. 2011, Welter-Schultes 2012, Araujo and de Jong 2015; Appendix S1: Table S1). Subsequently, a worldwide literature survey was performed using the Google Scholar search engine (<https://scholar.google.nl/>) and all scientific species name–environmental factor combinations (Table 1). Google Scholar ranked the hits based on their relevance to the performed query through determining publication location, authors, recent citations, and the number of citations (Google Scholar 2016). Subsequently, the first 50 hits of each search were assessed on their relevance for our research. In cases with fewer hits, all retrieved papers were assessed. In addition, several non-digitalized scientific books and journal issues available in the library of Radboud University were reviewed for relevant data. All retrieved data and references were entered in a database. In total, 493 papers (Appendix S2: Table S1) were considered relevant for this study. The resulting database consisted of 8405 entries on field occurrence and/or laboratory tolerance of species in combination with environmental factor levels. Data on environmental factors measured at the same sampling site and date where a species was found were classified as habitat

measurements. Measurements were classified as water body based when they characterized the environmental conditions of a water body where a species occurred without connection to a specific sampling site or habitat of a species.

Deriving environmental sensitivities

When more than five entries for a species were available, the range of occurrence was derived using environmental measurements in (1) habitats and (2) water bodies in which this species was present. For water depth and flow velocity, only field occurrence data could be used due to a limited number of laboratory studies (Table 1). Because no field data were available, air exposure tolerances were based on laboratory data regarding species mortality during air exposure at various air temperatures and relative humidity conditions. Laboratory data were also available for maximum temperature and minimum dissolved oxygen tolerances, and experimental conditions between laboratory studies varied slightly. No distinction was made between subspecies due to limited data availability. The worldwide search was restricted to native or alien freshwater species that occur in Europe. Data on occurrence and environmental tolerance of these species on other continents were included since these values delineate their global range of occurrence. Data on species occurrence concern lacustrine, riverine, and brackish ecosystems.

Deriving species sensitivity distributions

The minimum and maximum field-based occurrence and the laboratory-based tolerances of species were used to construct SSDs. The mean and standard deviation of an SSD depict the average and variation in range of occurrence or tolerance of species, respectively. The SSD can subsequently be used to predict the fraction of bivalve species predicted to be absent, expressed as the potentially not occurring fraction (PNOF) at specific levels of environmental factors. The standard deviation of the SSD is inversely proportional to the effect of a change in the environmental factor level on the fraction of absent species. The minimum number of species for deriving an SSD was eight, which was in accordance to the minimum sample size required for chemicals by the US Environmental Protection

Table 1. Overview of search terms used for data collection, number of papers and data entries on field occurrence, and laboratory tolerance of European bivalve species (presence–absence) in relation to various environmental factors.

Environmental factor	Search term “Scientific species name” and	Database		Derived sensitivities			
		Included papers (<i>n</i>)	Entries (<i>n</i>)	Lower limit	Upper limit	Data source	Endpoint
Water temperature	Temperature	311	2009	×	×	Field	Habitat range
				×	×	Field	Water body range
			939		×	Laboratory	Tolerance
Water depth	Depth	257	2899	×	×	Field	Habitat range
Air exposure	Desiccation	16	518		×	Laboratory	Tolerance
Oxygen availability	Oxygen	178	1422	×		Field	Habitat range
				×		Field	Water body range
			72	×		Laboratory	Tolerance
Flow velocity	Flow velocity	84	546	×	×	Field	Water body range†

Note: “×” signifies sufficient data available to derive species sensitivity distributions for lower and/or upper limits of field- or laboratory-based data.

† Only a limited number of entries for habitats were available, and these data were therefore combined with water body range data.

Agency and by the European Union (Del Signore et al. 2016a). Data for SSDs were checked for normal distribution using the `shapiro.test` function in R (R Core team 2014). Data that were not normally distributed were log10 transformed and subsequently checked for normality. Hereafter, SSDs were constructed for each environmental factor. A normal distribution was fitted to the acquired ranges of occurrence and laboratory-based tolerances for each environmental factor using the `fitdistrplus` package in R-statistics (Delignette-Muller and Dutang 2014, R Core Team 2014, Szöcs 2015). The 2.5% and 97.5% confidence intervals were derived using a bootstrapping function with one thousand iterations. Minimum flow velocity, minimum water depth, and minimum dissolved oxygen for field data were not normally distributed. The lack of normality was due to several species with a minimum occurrence of zero, thus not being limited by a minimum value of a specific environmental factor. In order to include these insensitive species in the SSD, normal distributions were fitted to the minimum flow velocity, depth, and dissolved oxygen data. This approach provides the most ecologically relevant result as the SSD attributes the potential presence of a representative part of the species pool independent of the environmental factor level and reflects the insensitivity of a part of the species pool to certain environmental factors. Robustness of the

constructed SSDs was analyzed (Appendix S3: Figs. S1–S5).

Statistical analyses and overall sensitivity

Means of SSDs were compared using the independent sample t-test. Slopes, expressed as the standard deviations, were compared using the Levene’s test. Comparisons were made between habitat- and water body-based SSDs, and when sufficient data available also comparisons between field- and laboratory-based SSDs. In addition, the SSDs of native and alien species were compared. Differences between parameters were considered significant when below the critical *P*-value of 0.05. Moreover, linear regression analyses were performed between habitat-based and water body-based occurrences (Appendix S1: Table S3).

Overall sensitivity of each species regarding the assessed environmental factors was calculated in order to elucidate whether a specific species had a high or low overall sensitivity. The analyses for ranking species sensitivity to involved environmental factors consisted of four steps: (1) sub-setting the database to species for which habitat sensitivities were derived for all environmental factors (*n* = 19); (2) for each environmental factor, species were ranked based on their sensitivity and assigned a score; (3) summing up all assigned ranks of a single species for all seven environmental factors; and (4) dividing

the sum by the total number of ranks minus the number of included environmental factors yielding an overall sensitivity. Using this approach, species with the highest sensitivity received a score of 1 and the lowest received a score of 19 (Appendix S1: Table S4). In the case of minimum requirements of habitat factors, species with the lowest sensitivity received a score of 1 and the species with the highest sensitivity received a score of 19 (Appendix S1: Table S4). The overall species sensitivity ranged between zero and one, with zero indicating a species with a low sensitivity and one indicating a species with a high sensitivity to climate change-related environmental factors. In addition, a separate overall sensitivity of species was calculated for the minimum and maximum values of environmental factors at which they were recorded.

RESULTS

Water temperature

Based on the minimum and maximum temperature of habitats, the PNOF for bivalves was lowest at 15.0°C (Fig. 1A). Maximum habitat temperature records of bivalve species varied between 15.5 for *Pisidium personatum* and 37.0°C for *Corbicula fluminea* (Appendix S1: Table S1). The minimum habitat temperature was 0°C for *Pisidium amnicum* and *Sphaerium corneum*. The SSDs based on the maximum temperature ranges in habitats and water bodies did not significantly differ in average (t -value: -0.44 ; P -value: 0.66) and slope (F -value: 1.77 ; P -value: 0.19 ; Fig. 1B, Table 2). A significant linear relation was found between the maximum temperature in water bodies and the maximum temperature of habitats of species (P -value: <0.001 ; R^2 : 0.38 ; Appendix S1: Table S3). No relation was found between the minimum temperature in water bodies and the minimum temperature of habitats of species (P -value: 0.23 ; R^2 : 0.06 ; Appendix S1: Table S3). The mean of the laboratory-based SSD for temperature was significantly higher than the mean of the SSDs derived from maximum recorded values in habitats and water bodies (t -value: -5.92 and -6.00 ; P -value: 0.00 and 0.00 , respectively). However, the slope was not significantly different (F -value: 0.042 and 0.61 ; P -value: 0.84 and 0.44 , respectively). The mean of the alien species SSD for maximum habitat

temperature was significantly higher than the mean of the SSD for native species (t -value: 2.32 ; P -value: 0.04 ; Fig. 1C). No significant difference in slopes of these SSDs was found (F -value: 0.37 ; P -value: 0.55). The means and slopes of SSDs for minimum temperatures did not significantly differ between alien and native species.

Oxygen availability

The minimum dissolved oxygen level in habitats of bivalve species varied between 0 for *Mytilopsis leucophaeata* and 10 mg/L for *Pisidium nitidum* (Fig. 2). For the majority of the species, the minimum dissolved oxygen level in their water bodies was close to zero. The laboratory-based tolerances ranged between survival for weeks at 0 mg/L for *Anodonta anatina* and *Anodonta cygnea* up to a decreased ciliary beating at a minimum concentration of 2 mg/L for *Musculium transversum*. The mean and slope of the laboratory-based minimum dissolved oxygen tolerances of species were significantly lower compared to that measured in their habitats (t -value: -7.07 ; P -value: 0.00 and F -value: 5.05 ; P -value: 0.03 , respectively). The SSDs for water body-based minimum dissolved oxygen level had a significantly lower mean than habitat-based ones (t -value: -4.48 ; P -value: 0.00); however, their slope did not significantly differ. No apparent differences were found among the various bivalve families (Fig. 2; Appendix S1: Table S1). The mean and slope of SSDs for habitat-based minimum dissolved oxygen levels of alien and native freshwater bivalves did not significantly differ. A significant linear relation was found between the minimum dissolved oxygen level in water bodies and the minimum dissolved oxygen level of habitats of species (P -value: <0.01 ; R^2 : 0.36 ; Appendix S1: Table S3).

Water depth

Comparison of the SSDs for minimum and maximum water depth of habitats revealed that the PNOF of bivalve species was lowest at a water depth of 1 m (Fig. 3A, B). The minimum water depth of habitats was close to zero for the majority of the species, whereas the maximum water depth varied from 0.25 m for *Pisidium pseudosphaerium* up to 350 m for *Pisidium conventus* (Appendix S1: Table S1). The mean and slope

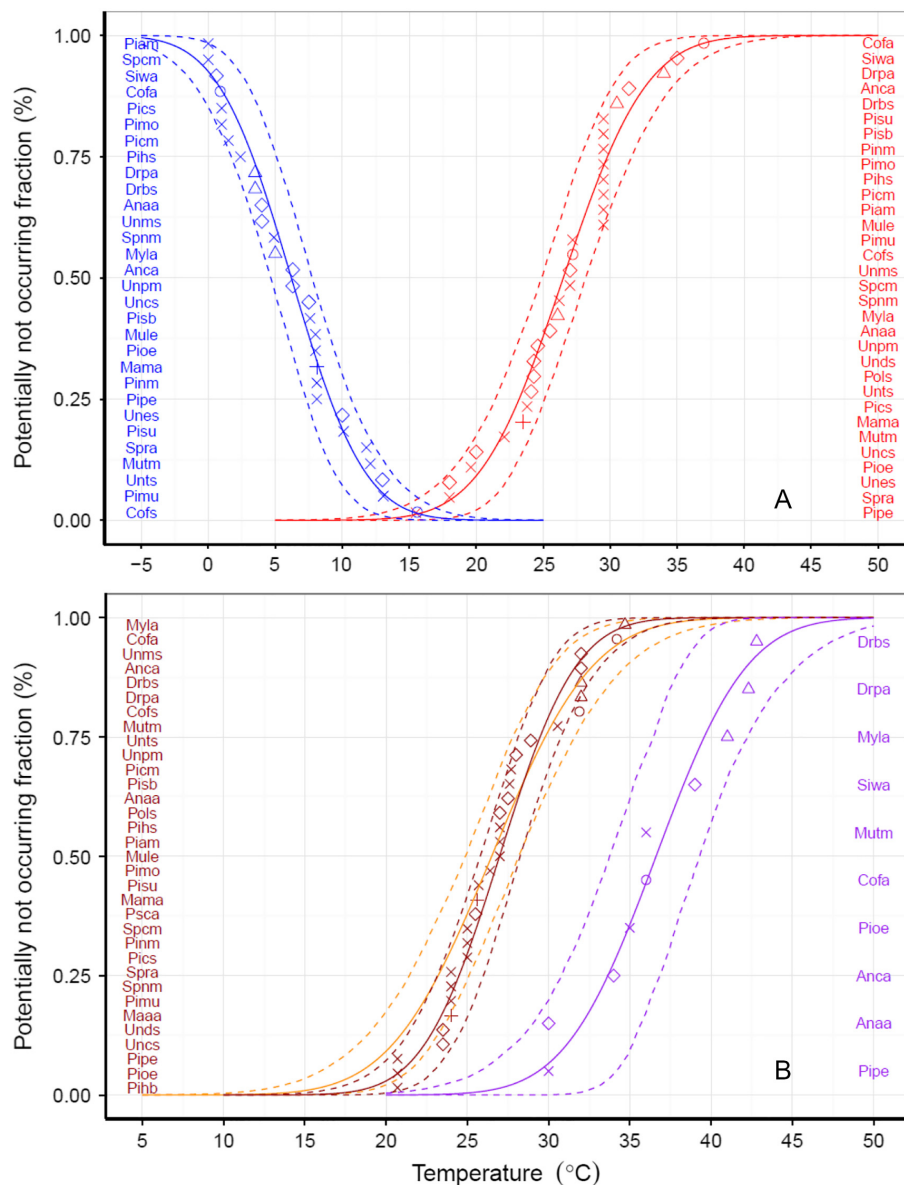
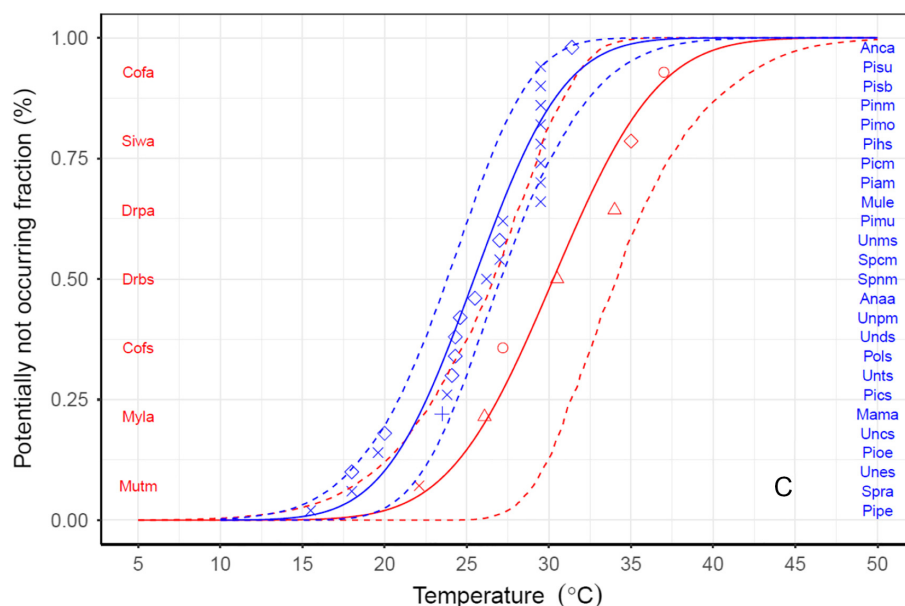


Fig. 1. Sensitivity distribution for (A) the minimum habitat temperature (blue line) and maximum habitat temperature (red line); (B) maximum habitat temperature (orange), maximum water body temperature (dark red), and maximum laboratory tolerance (purple); (C) the maximum habitat temperature of alien species (red line) and native species (blue line) of freshwater bivalve species and the 2.5% and 97.5% confidence intervals (dotted lines). The symbols represent species of the Corbiculidae (circles), Dreissenidae (triangles), Sphaeriidae (crosses), Unionidae (diamonds), and Margaritiferidae (plus signs). For each data point, the according species abbreviation is listed. Abbreviations of species are explained in Appendix S1: Table S1.

of SSDs for minimum and maximum water depth of habitats of alien and native freshwater bivalves did not significantly differ. All bivalve families were able to occur at shallow sites

(Fig. 3A). However, the Corbiculidae, Unionidae, and Margaritiferidae were not found to occur at depths deeper than 31 m, and Dreissenidae and several Sphaeriidae were recorded at depths



(Fig. 1. Continued)

deeper than 100 m, up to 150 and 350 m, respectively (Fig. 3B).

Flow velocity

For flow velocity, only few measurements in habitats of species were available. Therefore, available data for habitats and water bodies of each species were merged. Minimum flow velocity was 0 cm/s for the majority of the species and highest (5 cm/s) for *Unio crassus*. Maximum flow velocity ranged from 25 to 664 cm/s for *P. personatum* and *Unio tumidus*, respectively. The PNOF based on the minimum and maximum flow velocity was lowest at 10 cm/s and steeply increased with increasing flow velocities (Fig. 4A, B, Table 2). The mean and slope of SSDs for minimum and maximum flow velocity of alien and native freshwater bivalves did not significantly differ. No clear pattern was found between the occurrences of bivalve families and the minimum water body flow velocity (Fig. 4A). At high flow velocities in particular Unionidae occurred, for other families no clear patterns were found (Fig. 4B).

Air exposure

Only laboratory data were available for air exposure tolerances (i.e., vulnerability to

desiccation). Three invasive species (298 entries), namely *Dreissena polymorpha*, *Dreissena rostriformis bugensis*, and *C. fluminea*, were overrepresented in the laboratory data. Moreover, since air exposure tolerance depends on temperature and relative humidity, only tolerances derived under similar environmental conditions were used. As a result, air exposure data were derived for eight species at 20°C with a relative humidity ranging between 68% and 75% (Appendix S1: Table S5). The derived endpoints included the lethal time until 50% and 100% mortality (LT₅₀ and LT₁₀₀, respectively) for all eight species (Table 2; Appendix S2: Fig. S1).

Overall sensitivity

The rankings showed that *S. corneum* has the lowest overall sensitivity, indicating that this species has the broadest ranges of occurrences (Fig. 5A). Interesting to note is the low overall sensitivity of the invasive *C. fluminea* and *D. polymorpha*. The highest overall sensitivity was found for *Sphaerium rivicola*, a species that is vulnerable for extinction according to the IUCN red list (Appendix S1: Table S2). Two other endangered species, *U. crassus* and *Margaritifera margaritifera*, also have a high overall sensitivity (Fig. 5A). *S. rivicola* has the highest overall sensitivity when

Table 2. Data sources, endpoints, mean with standard deviation and standard error for species sensitivity distributions (SSD) of freshwater bivalve species for minimum and maximum of various environmental factors in their habitats and water bodies, and for laboratory-derived tolerances.

Environmental factor	Data source	Endpoint	Unit	Number of species (<i>n</i>)	SSD parameters				Normal distribution		
					Mean	Standard error (SE)	Standard deviation	SE	W-value†	P-value	Log ₁₀ transformed
Water temperature	Field	Minimum habitat occurrence	°C	30	6.20	0.78	4.29	0.55	0.95	0.19	No
	Field	Maximum habitat occurrence	°C	32	26.5	0.86	4.88	0.66	0.97	0.55	No
		Alien species	°C	8	30.27	1.89	5.01	1.34	0.96	0.78	No
		Native species	°C	24	25.44	0.86	4.29	0.61	0.90	0.02	No‡
	Field	Minimum water body occurrence	°C	30	1.11	0.28	1.54	0.20	0.81	0.00*	No‡
	Field	Maximum water body occurrence	°C	33	27.0	0.64	3.70	0.46	0.95	0.13	No
	Laboratory	Tolerance	°C	10	36.6	1.39	4.40	0.98	0.93	0.42	No
Water depth	Field	Minimum habitat occurrence	m	37	0.14	0.06	0.34	0.04	0.42	0.00*	No‡
	Field	Maximum habitat occurrence	m	37	1.22 (16.6)	0.11	0.64 (4.37)	0.07	0.96	0.26	Yes
Air exposure	Laboratory	LT ₅₀	h	8	125	33.3	94.1	23.5	0.89	0.24	No
	Laboratory	LT ₁₀₀	h	8	252	61.2	173	43.3	0.93	0.54	No
Oxygen availability	Field	Minimum habitat occurrence	mg/L	26	4.80	0.50	2.54	0.35	0.96	0.45	No
	Field	Minimum water body occurrence	mg/L	26	1.75	0.45	2.28	0.32	0.68	0.00*	No‡
	Laboratory	Tolerance	mg/L	8	0.76	0.25	0.69	0.17	0.91	0.33	No
Flow velocity	Field	Minimum water body occurrence	cm/s	23	1.00	0.30	1.44	0.21	0.73	0.00*	No‡
	Field	Maximum water body occurrence	cm/s	23	2.00 (99.7)	0.07	0.34 (2.18)	0.05	0.94	0.23	Yes

Note: Non-transformed values are depicted within brackets. LT₅₀, lethal time until 50% mortality; LT₁₀₀, lethal time until 100% mortality.

* Data not normally distributed, $P < 0.05$.

† W-value of Shapiro-Wilk test for normality

‡ Normal distribution was fitted as this provided the most ecological sound result.

only minimum sensitivities are taken into account (Fig. 5B). When only maximum sensitivities are taken into account, *D. polymorpha* has the lowest overall sensitivity, whereas *M. margaritifera* has the highest overall sensitivity (Fig. 5C).

DISCUSSION

Data deficiency and uncertainty

For the first time, SSDs of European freshwater bivalve species were derived for environmental factors that are affected by climate change. Despite acquiring 8405 data points, data were still lacking for several bivalve species. Minimum

and maximum water depth of habitats have been acquired for 37 (66.1%) of 56 freshwater bivalve species that currently occur in Europe. Data on minimum and maximum habitat temperature, dissolved oxygen level, and flow velocity have been acquired for 32 (57.1%), 26 (46.4%), and 23 (41.1%) species, respectively. For only 8 (14.5%) of the European freshwater bivalve species, air exposure tolerance data were available. For species with a restricted distribution and high conservation status, there was particularly limited data availability (Appendix S1: Table S1). It is important to study the range of occurrence of species for which this information is lacking (e.g.,

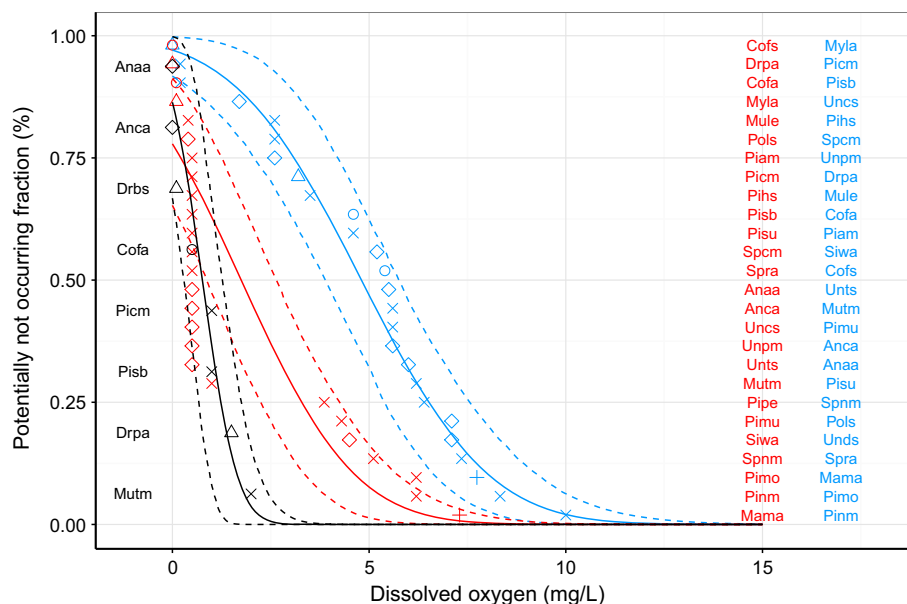


Fig. 2. Sensitivity distribution for the minimum dissolved oxygen level in habitats (light blue) and water bodies (red), and laboratory-derived tolerances (black) of freshwater bivalve species and the 2.5% and 97.5% confidence intervals (dotted lines). The symbols represent species of the Corbiculidae (circles), Dreissenidae (triangles), Sphaeriidae (crosses), Unionidae (diamonds), and Margaritiferidae (plus signs). For each data point, the according species abbreviation is listed. Abbreviations of species are explained in Appendix S1: Table S1.

Margaritifera auricularia, *Unio gibbus*, and *Pisidium edlaueri*), as this allows for adequate and efficient conservation efforts.

Besides the lack of data for some species, another uncertainty was the variation among measurements of environmental factors and the lack of precise description of measurement procedures. Therefore, standardized protocols should be developed and used to monitor the physicochemical characteristics of habitat of species in a consistent way (Parsons et al. 2002, Hering et al. 2003).

The occurrence range of each species was based on the highest or lowest measured field values for each environmental factor, indicating that this species was not found at more extreme levels. Laboratory-derived tolerances have additional value but also their own limitations and may differ depending on the experimental setup (Kefford et al. 2004), experimental duration (Van den Brink et al. 2006, Brix et al. 2011, Santos et al. 2011), acclimatization time to environmental conditions such as temperature and warming rate (Hathaway 1928, McMahon 1996), and the

origin of species (Larras et al. 2016). Field-based environmental ranges of species occurrences may be more realistic to actually occurring environmental conditions compared to tolerances obtained in laboratory tests (Leung et al. 2005). However, effects of extreme events cannot be predicted by field data only. Laboratory-derived tolerances under extreme conditions can give an indication of species performance during extreme events with a limited time frame.

Under field conditions, species can be limited by several environmental factors that act independently or in combination (De Zwart and Posthuma 2005, Webb et al. 2008, Tockner et al. 2010). Our approach to derive occurrence ranges for each environmental factor separately does not take these interacting effects into account. However, by using occurrence data from the entire known distribution of each species the chance of having a location, both in time and space, where only one of the studied environmental factors is limiting increases. Thus, the presented environmental ranges of occurrence are likely to represent the effect of one

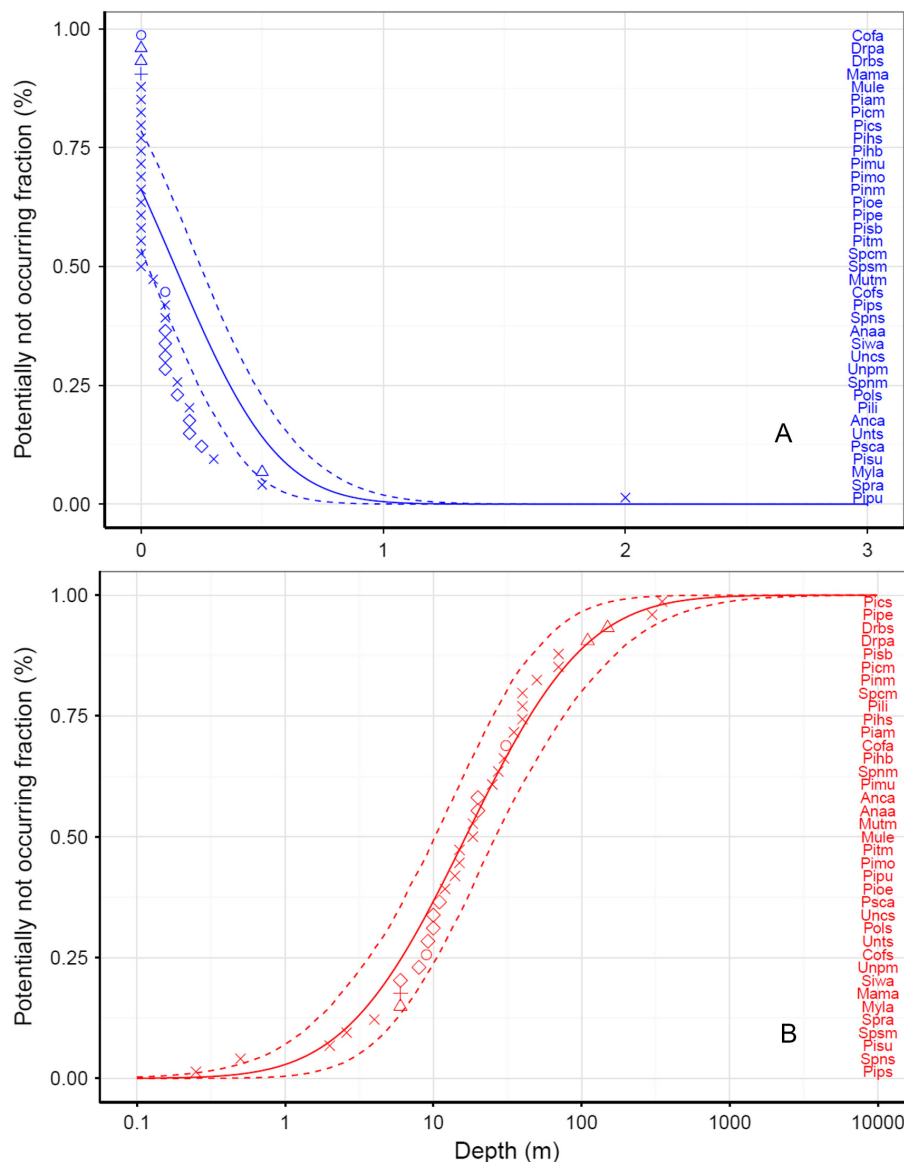


Fig. 3. Sensitivity distribution for (A) the minimum habitat water depth of habitats (blue line); (B) the \log_{10} transformed maximum water depth of habitats (red line) of freshwater bivalve species and the 2.5% and 97.5% confidence intervals (dotted lines). The symbols represent species of the Corbiculidae (circles), Dreissenidae (triangles), Sphaeriidae (crosses), Unionidae (diamonds), and Margaritiferidae (plus signs). For each data point, the according species abbreviation is listed. Abbreviations of species are explained in Appendix S1: Table S1.

environmental factor at a time. Therefore, future studies that aim to derive field-based environmental range of occurrence should not limit the data to a specific geographic region, but include all environmental parameter measurements in combination with occurrence data across the known distribution of the assessed species.

The derived presence/absence data and thus the environmental range of occurrence are based on adult individuals. For fish, earlier studies have shown that there is a difference in sensitivity between different life stages to dissolved oxygen (Elshout et al. 2013). For bivalve species, often no indication of the life stage of the found

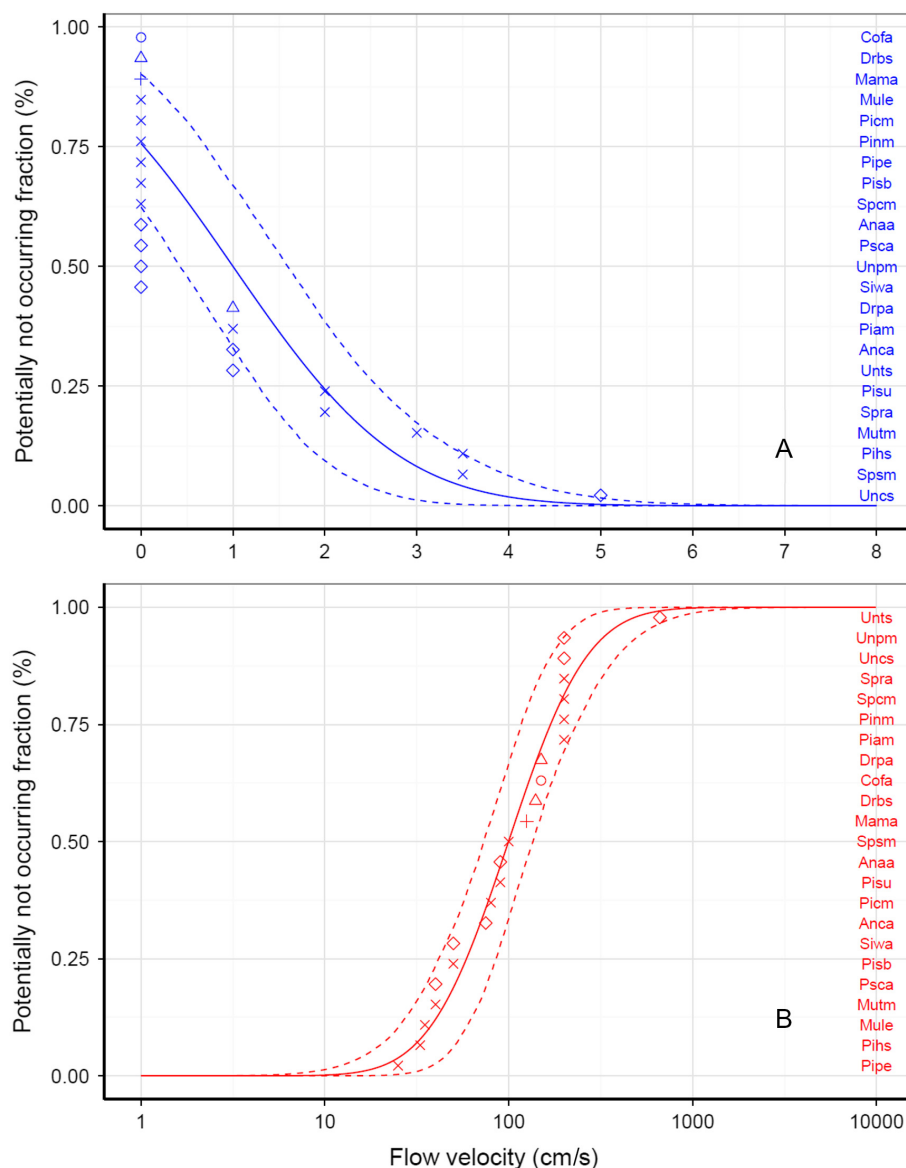


Fig. 4. Sensitivity distribution for (A) the minimum water body flow velocity (blue line) and (B) the log₁₀ transformed maximum water body flow velocity (red line) of freshwater bivalve species and the 2.5% and 97.5% confidence intervals (dotted lines). The symbols represent species of the Corbiculidae (circles), Dreissenidae (triangles), Sphaeriidae (crosses), Unionidae (diamonds), and Margaritiferidae (plus signs). For each data point, the according species abbreviation is listed. Abbreviations of species are explained in Appendix S1: Table S1.

species was given, and the assumption was made that all reported presence/absence data were based on adults, unless clearly stated. Thus, there is an urgent need for environmental occurrence data for different life stages of bivalve species, as an increased knowledge will aid to setup

conservation measures to ensure a healthy population of endangered species. This especially holds for glochidia, the parasitic life stage of unionids, that mature attached to the gills of freshwater fish and are expected to have different sensitivities compared to adults.

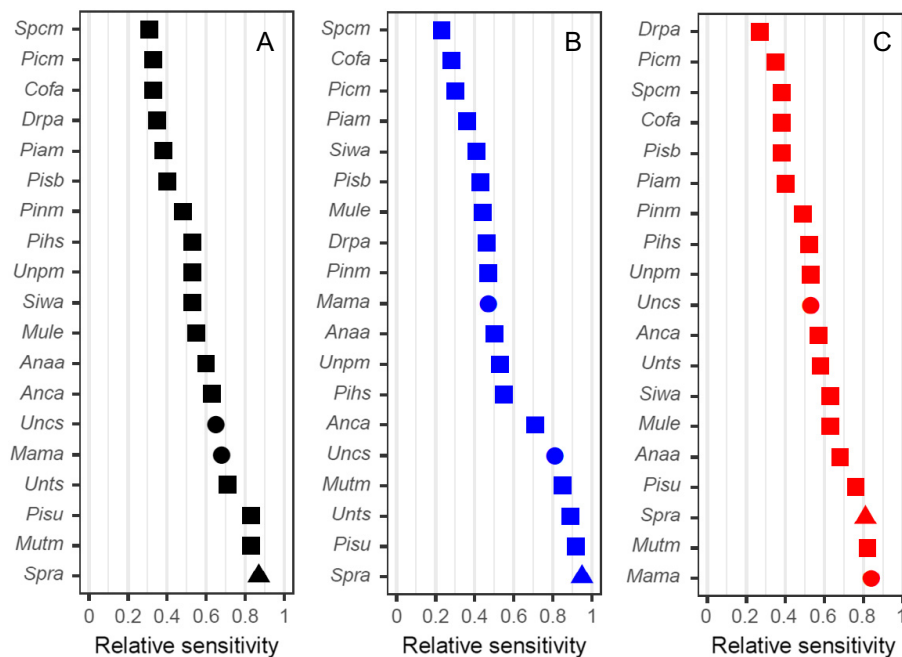


Fig. 5. Overall sensitivity of freshwater bivalves to climate-related environmental factors for (A) both minimum and maximum sensitivities; (B) minimum sensitivities and (C) maximum sensitivities. The symbols represent the status of the species on the IUCN red list: least concern (square), vulnerable (triangle), and endangered (circle). For each data point, the species abbreviation is listed. Abbreviations of species are explained in Appendix S1: Table S1.

Water temperature

The comparison between laboratory- and field data-based SSDs showed that the mean of temperature-based SSDs depends on the data source. However, the slope of the laboratory- and field data-based SSDs did not differ statistically, indicating that water body temperatures can be used as an indication of habitat sensitivities. This is supported by the linear relation found between the maximum temperature in water bodies and the maximum temperature of habitats of species, indicating that the same approach can be used on a species level. A study regarding the field data-based temperature sensitivities of freshwater fish by Leuven et al. (2011) found the same mean minimum and maximum sensitivity compared to our habitat sensitivities (6°C and 26.6°C for fish and 6.2°C and 26.5°C for bivalves). The slope of maximum temperature sensitivities of freshwater fish was larger compared to the variation among bivalve sensitivities (6.55 and 4.88 for fish and bivalves, respectively). Since the slope is a measure for the effect of changing

environmental conditions on the species pool, the similarity indicates that the PNOF increases with the same rate, independent of the used sensitivity endpoint. A similar pattern is visible between laboratory- and mesocosm-derived sensitivities for several chemicals (Hose and Van den Brink 2004, Maltby et al. 2005). However, the laboratory tolerances are based on different endpoints (e.g., mortality and loss of ciliary function), thereby limiting the use of the laboratory data-based SSDs. The mean of the maximum habitat temperature for alien species was significantly higher than that for native species, which was also found for mollusk species inhabiting the river Rhine (Verbrugge et al. 2012). Because climate change is expected to increase water temperatures (Quayle et al. 2002, Adrian et al. 2009, Van Vliet et al. 2013), a higher fraction of native species will potentially not occur in future situations compared to alien species. Previous research has shown that under the expected climate change, the native *Pseudanodonta complanata* (Rossmassler, 1835) would experience a

decreasing range size, whereas the alien *Dreissena polymorpha* would have an increased range size (Gallardo and Aldridge 2013). As the slope of both SSDs did not differ, the increase in PNOF will be equal for both species groups.

Oxygen availability

The mean of the minimum habitat dissolved oxygen and minimum water body dissolved oxygen SSD were significantly different. This is likely caused by lower sampling efforts during cold months resulting in higher minimum habitat dissolved oxygen levels compared to the water body range of occurrence. Though, the linear relation found between the minimum dissolved oxygen level in water bodies and the minimum dissolved oxygen level of habitats of species is an indication of the minimum dissolved oxygen level of a species based on the water body of occurrence. The minimum habitat dissolved oxygen and minimum water body dissolved oxygen SSD had a different mean and slope compared to minimum dissolved oxygen laboratory tolerances. The difference in shape is likely caused by the fact that dissolved oxygen concentration itself cannot go lower than zero, skewing the variation among water body range of occurrence toward one side. However, the laboratory tolerances are based on mortality, prolonged survival of the anoxic conditions, and decreased ciliary function endpoints, thereby limiting the use of the laboratory data-based SSDs.

Dissolved oxygen concentration depends on environmental conditions. The overexploitation of water and modification of flow can result in stagnant waters that have a decreased dissolved oxygen concentration (Baxter 1977, Gagnon et al. 2004). With increasing temperatures, the solubility of oxygen decreases (Weiss 1970), decreasing the dissolved oxygen concentration. Moreover, pollution and eutrophication negatively impact the dissolved oxygen concentration in freshwater (Sánchez et al. 2007).

Not only is there *de facto* an effect of environmental factors on dissolved oxygen concentration, but also a combined effect of environmental factors on the tolerance of species. Recently, thermal tolerance of several freshwater ectotherms was found to be dependent on oxygen availability (Verberk and Bilton 2011, Verberk and Calosi

2012, Verberk et al. 2016). An effect of oxygen availability on thermal tolerance was also found for several freshwater gastropods (Koopman et al. 2016) and for a marine bivalve (Pörtner et al. 2006). Therefore, an attempt should be made to characterize the interacting effect of oxygen and temperature on freshwater bivalve tolerances and ranges of field occurrence.

Water depth

Freshwater bivalve species were found to inhabit a wide range of depths, ranging from shallow temporary pools with a depth of 0.25 m up to 350 m in lakes. Species with a narrow depth distribution will likely be more affected with the increasing variability in river discharges (Watson 2001, Sophocleous 2004) also influencing the water level in lakes and ponds. Under low discharge conditions, the species that occur in the littoral zone will be more affected compared to species that can occur in deeper waters or will migrate to deeper waters. The difference in shape between the minimum and maximum depth is likely caused by the fact that minimum depth cannot go lower than zero, reducing the variation among minimum depths.

Air exposure

Desiccation by air exposure was found to be the main environmental factor limiting the occurrence of bivalve species in rivers, lakes, and wetlands (Collas et al. 2014, Leuven et al. 2014). An increase in the frequency and intensity of droughts due to climate change is expected (Lehner and Döll 2001). Because data on effects of air exposure are relatively scarce (Tables 1 and 2), there is an urgent need to assess air exposure tolerance of freshwater bivalve species.

Flow velocity

The difference in shape between the minimum and maximum flow velocity is likely caused by the fact that minimum flow velocity cannot go lower than zero, reducing the variation among minimum flow velocities. No difference was found between SSDs for alien and native freshwater bivalves.

Overall sensitivity

The analyses of overall species sensitivity increase understanding about which species will

be affected by climate change. Our results show that endangered species (e.g., *Unio crassus*, *Margaritifera margaritifera*, and *Sphaerium rivicola*) will experience a high pressure by climate change, likely further decreasing their populations. The effect of climate change on occurrence of invasive species (*C. fluminea* and *D. polymorpha*) is expected to be low. These species are already widely spread.

Application

The derived SSDs can be used to determine the PNOF due to environmental conditions in a specific region (de Vries et al. 2008, Leuven et al. 2011, Verbrugge et al. 2012, Collas et al. 2014). When the environmental conditions of a site are known in detail, a spatial analysis can be made of potential habitat suitability. Provided that endpoints are explicit and comparable, combining the potential habitat suitability of several environmental factors enables managers and researchers to pinpoint possible hotspots for local biodiversity. Though, caution is required as the interaction between environmental factors is not taken into account. The habitat suitability of freshwater ecosystems for bivalve species can be optimized using the SSDs to guide the physical reconstruction and management of habitats. For instance, shipping-induced variability in flow velocity in littoral zones of regulated rivers can be mitigated by replacing groynes by longitudinal training dams (Del Signore et al. 2016b, Collas et al. 2018). At a species-specific level, the same approach can be used to a priori optimize habitats or to mitigate dominance of invasive bivalve species by taking the species-specific sensitivities for environmental conditions into account. Even at larger spatial scales, SSDs can be applied to determine the effects of future climate change on freshwater bivalve assemblages. Potentially not occurring fraction calculations for multiple environmental factors allow rankings of these factors and identification of the most limiting factor (Fedorenkova et al. 2012). Moreover, the derived environmental range of occurrence and tolerances of individual species can also be used to determine the species that are most vulnerable to climate change. This can be done for a combination of a single environmental factor and specific species, but also by taking all environmental factors and species into account using an

overall sensitivity approach as demonstrated in this study. Applicability of the derived environmental range of occurrence is not limited to Europe as several species assessed originate from other continents (*C. fluminea*, *Musculium transversum*, *Sinanodonta woodiana*) or are invasive alien species at other continents (e.g., *D. polymorpha*, *Dreissena rostriformis bugensis*, and *C. fluminea*; Appendix S1: Table S3). Therefore, the present results are relevant for all continents. The application of combining the sensitivity to single environmental factors into an overall sensitivity allows for an integrated assessment of multiple environmental factors. An overall sensitivity analysis enables the prioritization of species that urgently require conservation measures to prevent their demise.

CONCLUSION

Using an extensive database, novel species sensitivity distributions (e.g., for water temperature, water depth, flow velocity) can be derived that can be used to estimate potential not occurring fractions of species pools in Europe. The data also allow to calculate the overall sensitivity of species to all assessed environmental factors allowing to predict which species will be most affected by climate change. The distinction between habitat- and water body-based data points proves unnecessary for deriving water temperature sensitivities. Though, for dissolved oxygen-level sensitivities, water body data points result in a lower sensitivity. After analyzing data deficiencies in the dataset, we recommend characterizing the environmental range of rare and endangered freshwater bivalve species both from a conservation and restoration perspective. Moreover, research should be performed on deriving ranges of occurrence for various bivalve life stages and other species groups of freshwater invertebrates (e.g., Gastropoda and Decapoda). As several environmental factors interact, the combined effect of multiple environmental factors on the range of occurrence and tolerance of species should also be assessed.

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